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REPRODUCTIVE ECOLOGY OF DUSKY FLYCATCHERS IN WESTERN MONTANA

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ABSTRACT.—Breeding ecology of Dusky Flycatchers (*Empidonax oberholseri*) was studied in western Montana from May–August 1974. Dusky Flycatchers were monogamous and single-brooded although some pairs made renesting attempts after first nests failed. Length of the reproductive cycle for first nesting attempts, from arrival on the breeding grounds to fledging, was about 70 days. All nests were placed in shrubs, primarily ninebark (*Physocarpus malvaceus*) and Rocky Mountain maple (*Acer glabrum*), and were an average of 150 cm above the ground. Females incubated a clutch with an average of 4.0 eggs for 15–16 days, and the average nestling period was 17.5 days. Both sexes fed nestlings and fledglings, but only females brooded nestlings. Egg survival was 63.8%, hatching success was 95.4%, and nestling survival was 61.9% for an overall probability of 0.376 that an egg produced a fledgling. Predation was the major cause of nest failure. Dusky Flycatchers reared an average of 1.9 fledglings/pair. *Received 14 Jan. 1992, accepted 28 May 1992.*

The Dusky Flycatcher (*Empidonax oberholseri*) is a common breeding species throughout much of the mountainous western United States. It occurs in open coniferous forest, mountain chaparral, aspen groves, willow riparian, and in brushy open areas, often with trees scattered throughout the habitat (Grinnell et al. 1930, Sedgwick 1975, A.O.U. 1983). There is little published information on the species; major sources include Bowles and Decker (1927), Bent (1942), Johnson (1963), and Morton and Pereyra (1985). The natural history of this species is poorly known or is anecdotal, although extensive information is presented in Johnson (1963) on morphology, plumages, distribution, behavior, and vocalizations. I report here on various aspects of the breeding biology of the Dusky Flycatcher, including nesting success, nest-site selection, reproductive chronology, and brood parasitism.

STUDY AREA AND METHODS

The study was conducted from 1 May–15 August 1974 at three study sites in the Lolo National Forest, Missoula County, Montana. Elevations ranged from 1066 to 1280 m and the dominant overstory vegetation was mixed ponderosa pine/Douglas-fir (*Pinus ponderosa*)/(*Pseudotsuga menziesii*). Trees in portions of each study area had been thinned so that study sites included coniferous forest, shrubby openings with scattered trees, and intermediate edge sites. Common understory shrubs included Rocky Mountain maple (*Acer glabrum*), mallow ninebark (*Physocarpus malvaceus*), russet buffaloberry (*Shepherdia canadensis*), common chokecherry (*Prunus virginiana*), Saskatoon serviceberry (*Amelanchier alnifolia*),

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common snowberry (*Symphoricarpos albus*), Woods rose (*Rosa woodsii*), and bearberry manzanita (*Arctostaphylos uva-ursi*). The herbaceous layer was characterized by pine reedgrass (*Calamogrostis rubescens*), elk sedge (*Carex geyeri*), bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), heartleaf arnica (*Arnica cordifolia*), and arrowleaf balsamroot (*Balsamorhiza sagitatta*).

Nests were located by searching in suitable habitats, observing adults during nest construction, following adults with food, or observing males feeding incubating females. Nests were checked at least every third day; most were visited daily. Some nests were observed intensively with a 20× telescope, usually from < 15 m. Nest and bush heights were measured after completion of the nesting cycle. Nest dimensions were measured before nestlings hatched and before nests were altered by compaction by nestlings and females. Seventeen nests were collected and later analyzed for composition.

Individual birds were not marked for this study. Because Dusky Flycatchers are sexually monomorphic, I assumed that males performed advertising songs and incubation feeding and that females performed incubation duties. At some nests females were positively identified from their behavior, and slight differences in plumage characteristics (mostly differences in the extent of the eye ring and the extension of the eye ring forward to the lore) allowed me to distinguish between the sexes. Numerous subsequent observations at nests where the female was positively identified confirmed that it was the female incubating and the other member of the pair performing advertising songs and incubation feeding duties. Weather data were obtained from the National Weather Service Office in Missoula, ≤24 km from study sites. Statistical significance was set at $P \leq 0.05$.

RESULTS AND DISCUSSION

Reproductive chronology.—The first *Empidonax* flycatchers in 1974 arrived in western Montana on 7 May. Because these birds were silent and furtive, I could not distinguish Dusky Flycatchers from Hammond's (*E. hammondii*), Least (*E. minimus*), Willow (*E. traillii*), or Alder (*E. alnorum*) flycatchers, all of which breed in or migrate through western Montana. By 14 May, males began giving "du-hic" vocalizations (after Johnson 1963) and were positively identified as Dusky Flycatchers. Advertising songs were first heard on 17 May, although non-territorial migrant *Empidonax* flycatchers were still moving through the area as late as 16 May. In the northern Sierra Nevada, Dusky Flycatchers usually arrive in the second week of May (Johnson 1963).

Dusky Flycatchers began building nests about 1 June. Several nests (N = 11) were located before eggs were laid, including two nests found on 3 June with approximately one third of the nest mass in place. The first egg in each of these nests was not laid until 15 June. Allowing two days to complete the first third of the nest, the time between nest initiation and laying was about 14 days. The mean date for laying egg 1 (N = 11 nests) was 11 June (range: 31 May–16 June); by back-dating, the average date of nest initiation was 28 May.

Whereas the period between nest initiation and egg laying may be quite extended, the nest appears to be built in only a few days. One nest, for example, was in the early stages of construction on 9 June, appeared complete on 11 June, but did not receive any eggs until 17 June. The only changes in the nest between 11 and 17 June were the addition of a few feathers and bud scales to the lining. Cool, rainy weather in late May and early June may have slowed nest building and egg laying. From 20 May–10 June, the mean daily temperature was below normal on 14 of 22 days and precipitation was recorded on 14 of those 22 days.

The mean date of clutch completion for first nests (N = 11) was 14 June (range: 3 June–19 June). The mean date of hatching of the last egg (N = 10) was 28 June (19 June–4 July) and the mean date the last nestling fledged was 13 July (N = 9, 5–21 July). Thus, the entire reproductive cycle for first nest attempts, from arrival on the breeding grounds to fledging, was about 70 days. The interval from arrival to nest initiation was 21 days; nest initiation to laying of the first egg took 14 days; the egg-laying sequence required 4–5 days (N = 6); incubation lasted 15–16 days (N = 9), and the mean time from hatching of the last egg to fledging of the last young was 15.6 days (N = 7, range: 13–18 days).

Nest site selection.—All nests found (N = 25) were in shrubs, although the species also nests in aspens (Sumner and Dixon 1953) and small conifers (Bent 1942, Johnson 1963, Morton and Pereyra 1985). Most nests were in mallow ninebark (48%) or Rocky Mountain maple bushes (44%); one nest was in a common chokecherry bush and one was in a russet buffaloberry bush. Mean height of nests was 150.7 ± 14.4 cm [SE] (70.1–347.5 cm) which generally agrees with the findings of others (e.g., Sumner and Dixon 1953, Johnson 1963, Manuwal 1968). Mean nest bush height was 256.4 ± 26.0 cm (91.4–548.6 cm). Mean bush heights of the two most commonly used bush species differed (ninebark: $\bar{x}$ = 153.2 ± 10.7 cm vs mountain maple: $\bar{x}$ = 364.0 ± 31.1 cm, $P < 0.0001$) as did mean nest heights in those two species (ninebark: $\bar{x}$ = 101.9 ± 10.2 vs mountain maple: $\bar{x}$ = 204.5 ± 20.7 cm, $P = 0.0005$). These discrepancies suggest that birds select a relative height within a bush rather than height above the ground. Criteria used in selection might include an optimal stem structure for nest support, a position which results in concealment of nests from predators (Evans 1978), or a nest location which enhances the immediate thermal environment (Ricklefs and Hainsworth 1969). This is in concordance with nest : bush height ratios which were similar for ninebark and mountain maple (ninebark nest : bush height $\bar{x}$ = 0.67 ± 0.04 vs mountain maple nest : bush height $\bar{x}$ = 0.58 ± 0.05, $P = 0.17$). For all species of bushes, nest height tended to increase with bush height (nest height = 32.5 ± 0.46 × bush height, $R^2 = 0.69$, $P < 0.001$).

Nest dimensions and materials.—After flycatchers fledged, I collected 17 nests and analyzed their composition. Nests were soft, neatly woven cups built largely of grasses and finely shredded plant material. In a typical nest, this constituted most of the total nest mass. Frequently used materials included grass culms and blades, often shredded, forb stems, and the finely shredded bark of mallow ninebark. Most of the mass in three nests was deer (*Odocoileus* spp.) hair, which was also used in the lining of two other nests. Most nests (11/17) contained a number of feathers, including those of at least four different species of birds. The linings of 15 of 17 nests contained coniferous bud scales, and 15 of 17 nests also were lined with small amounts of lichen (*Usnea* sp.). Other less commonly used nest materials included needles of ponderosa pine and Douglas-fir, string, horsehair, bits of paper, and the pappus of Compositae.

Nest dimensions (N = 21) were: outside diameter (top of cup), $\bar{x} = 7.4 \pm 0.10$ cm (range = 6.7–8.2 cm), outside height, $\bar{x} = 7.2 \pm 0.13$ cm, (6.0–8.5 cm), inside cup diameter $\bar{x} = 5.3 \pm 0.08$ cm, (4.7–6.0 cm), inside cup depth $\bar{x} = 3.6 \pm 0.08$ cm, (2.8–4.5 cm). These dimensions are similar to those of Bowles and Decker (1927), Bent (1942), and Johnson (1963).

Clutches.—The number of eggs per clutch was 4.0 ± 0.0 (N = 21 nests) for first nest attempts. Two of three renest clutches contained four eggs, and one consisted of three eggs. Johnson (1963) also reported a clutch size of four (N = 7 nests found before hatching) but Bent (1942) reports the number as being three or four and sometimes only two. Bowles and Decker (1927) found one nest with five eggs, but all others contained four. Morton and Pereyra (1985) report a usual clutch size of three or four.

The duration of laying in Dusky Flycatcher females was 4–5 days. Eggs were laid on consecutive days at four of six nests where laying was followed closely. At two other nests, a day was skipped after laying of the second and third eggs, respectively. Similarly, Davis et al. (1963) reported that for seven of nine nests of the Western Flycatcher, one day was skipped in the laying sequence.

The eggs were ovate, creamy white, and had little gloss. None of the eggs (N = 95) had any markings although those of some *Empidonax* flycatchers are lightly to heavily marked at the large end (Bent 1942). Of 43 eggs measured from 11 different nests, mean length × width was $17.8 \pm 0.12 \times 13.4 \pm 0.05$ mm. This compares with 50 eggs reported in Bent (1942) averaging 17.3 × 13.4 mm. Eggs having extreme lengths and widths measured 19.6 × 13.2, 18.9 × 14.0, 15.5 × 13.0 and 16.0 × 12.8 mm.

Incubation.—Incubation was performed by the female alone (Johnson 1963, Morton and Pereyra 1985) as in most *Empidonax*. Incubation began no later than after the laying of the second egg. Two lines of evidence support this: (1) seven of nine nests followed closely during laying were attended by females for extended periods after laying of the second egg, and (2) in seven of 10 nests the first two eggs laid hatched on the same day and 1–2 days before the third and fourth eggs hatched. In three other nests, egg 1 hatched one day earlier than egg 2, suggesting incubation began as early as the first day of laying. Three of the seven females attending nests with two eggs were being fed by males, which further corroborates extended nest attendance after laying of the second egg. King (1955) observed some Willow Flycatcher females incubating after laying the second egg, whereas Davis et al. (1963) reported "heavy" incubation beginning with completion of the clutch in the Western Flycatcher. Morton and Pereyra (1985) found that Dusky Flycatchers regularly tended eggs in the daytime after the laying of the second egg but that eggs were not maintained for long periods at temperatures necessary for embryonic growth.

The incubation period lasted 15–16 days. At four of six nests, the incubation period was 15 days (days from laying of the last egg to hatching of that egg). At two other nests, the incubation period was at least 15 and at least 16 days, respectively. Bent (1942) reported the incubation period as "12 to 15 days" and "13 or 14 days", with one instance of 17 days. Johnson (1963) recorded the incubation period as 14 days for one nest and Morton and Pereyra (1985) reported a "usually observed" incubation period of 15 or 16 days.

Nest attentiveness of females with complete clutches averaged 86.0 ± 0.35% for 15 nests (39 h observation). This compares with an attentiveness of 77% for Hammond's (Davis 1954), 77.1% for Least (Davis 1959), and 77.1–80.6% for Western (Davis et al. 1963) flycatchers. In the eastern Sierra Nevada, mean attentiveness for Dusky Flycatchers for five nests for the full period of incubation was 75.8% (Morton and Pereyra 1985). In that study, total daytime attentiveness increased steadily with ambient temperature, and this relationship may explain the difference between attentiveness values in the Sierra Nevada and in Montana (this study). Mean 2-h-interval ambient temperatures during the warmest part of the day (13:00–17:00 h PDT) did not exceed 20°C in the Sierra Nevada, but in Montana during the primary period of incubation (14 June–14 July), the mean maximum temperature was 29.3°C. Because of higher ambient temperatures, there was likely an increased need to protect eggs from damage by solar heating in Montana. Mean attentive and inattentive bouts for Dusky Flycatchers averaged 21.0 and 6.6 min, respectively (this study) as compared to 19.3 and 6.8 min in the Sierra Nevada (Morton and Pereyra 1985).

Incubation feeding frequently occurs in Dusky Flycatchers (see further), and this inflated attentiveness values. At nests observed when incubation feeding occurred at rates >1 feeding/h ($N = 7$), attentiveness was higher than at nests where incubation feeding did not occur ($\bar{x} = 96.1 \pm 0.13\%$ vs $84.2 \pm 0.38\%$, respectively, $P = 0.036$).

Incubation feeding.—Incubation feeding, which I define as food-bringing by a male to an attending female, occurred frequently in Dusky Flycatchers. At 13 nests watched for extended periods during incubation, seven of 13 males (53.8%) were observed feeding incubating females. Incubation feeding occurred as early as the first full day of incubation (at 3 nests with 2 eggs present) and as late as the last day of incubation (at one nest on day 16 of incubation). Such feeding may also extend into the brooding period. This occurred at two nests (on the second and fourth days of brooding); during this period the female may eat the food herself (10/25 instances) or transfer it to a nestling (15/25 instances).

The mean rate of incubation feeding (N = 7 nests, incubation period only) was 5.38 ± 0.76 feedings/h (0.57 feedings/h [1 feeding in 105 min] to 13 feedings/h [13 feedings in 60 min]). Although others have observed incubation feeding in *Empidonax* flycatchers, only Manuwal (1968) and Morton and Pereyra (1985) have reported it in Dusky Flycatchers. Johnson (1963) observed it once in Gray Flycatchers, Davis et al. (1963) saw it once in Western Flycatchers, and Davis (1959) observed it 11 times in 6 h, and 12 times in 128 min at two nests of Least Flycatchers. It is apparently rare in the Tyrannidae (Skutch 1960).

The circumstances under which incubation feeding occurred were as follows: (1) the female was nearly always on the nest when the male arrived with food (the female was off on only one of 58 feedings), (2) the male directed feedings at the female's mouth, not at her back, (3) females accepted the food enthusiastically, (4) feedings occurred frequently, and (5) feeding was more common during early incubation than near hatching. These factors suggest that the function of incubation feeding in Dusky Flycatchers is not to learn when the eggs hatch; thus, incubation feeding in Dusky Flycatchers is not a type of anticipatory food bringing (Nolan 1958). Incubation feeding may help maintain the pair bond, however, and because attentiveness was higher at nests where incubation feeding occurred, incubation feeding may result in increased nest success.

Nestling period.—The average nestling period (time from hatching of the first egg to fledging of the last nestling) at nests where fledging occurred naturally (N = 8 nests) was 17.5 ± 0.63 days (range = 15–20 days). Grinnell et al. (1930) report a nestling period of 18 days. This compares with nestling periods of 14.5–17.5 days for the Western (N = 4) (Davis et al. 1963), 17–18 days for Hammond's (N = 2) (Davis 1954), and 12–13 days for Willow (King 1955) flycatchers. The individual nestling interval (after Nolan 1978), equivalent to nestling age at fledging, was 16.3 ± 0.33 (range = 14–18) days (N = 32 young). For Willow Flycatchers, Walkinshaw (1966) and Holcomb (1972a) report ages at fledging of 13.8 and 12.3 ± 0.1 days, respectively.

For first-hatched young, the average individual nestling interval was

16.9 ± 0.40 days and for fourth-hatched young it was 15.8 ± 0.45 days. This difference is marginally significant ($P = 0.085$) reflecting the fact that even though fourth-hatched eggs hatched 1–3 days after the first, the nestlings sometimes all fledged on the same day. Younger nestlings, while not as developed as older nestlings, probably reduce the risk of predation by leaving when older nestlings are motivated and in a condition to fledge (Nolan 1978). The interval between the fledging of first- and last-hatched nestlings varied from <4 min to >48 h (N = 8 nests).

Brood parasitism.—One of 24 (4%) Dusky Flycatcher nests was parasitized by Brown-headed Cowbirds (*Molothrus ater*); however, cowbirds were present on only one of the three study areas. Nine nests were found at that area, so the parasitism rate where both flycatchers and cowbirds were present was 11.1%. The parasitized nest was first found on 5 July, and contained four flycatcher eggs and one cowbird egg. A predator interfered at this nest and the cowbird nestling was last seen at 8 days of age. One flycatcher eventually fledged from this nest.

There are 11 previous records of parasitism by cowbirds on Dusky Flycatchers (Friedmann et al. 1977), but no published information on the frequency of parasitism for this species. Records of other *Empidonax* flycatchers being parasitized by cowbirds are not uncommon (i.e., Alder, Willow, Least, Gray [*E. wrightii*], Hammond's Western, Acadian [*E. virescens*], and Yellow-bellied [*E. flaviventris*] flycatchers) (Brandt 1947, Friedmann et al. 1977). As a group, *Empidonax* flycatchers are not parasitized heavily, but moderately high rates of parasitism have been reported for the Acadian (24%: Walkinshaw 1961), Traill's (superspecies) (21%: Hicks 1934; 20.8%: Berger and Parmalee 1952), and Willow (40.7%: Sedgwick and Knopf 1988) flycatchers. Where breeding densities of cowbirds are moderate to high, it appears that some *Empidonax* flycatchers are susceptible to considerable parasitism. At least some parasitism of Dusky Flycatchers probably occurs wherever circumstances bring Dusky Flycatchers and Brown-headed Cowbirds into contact.

Nesting success.—Of 95 eggs laid in 24 nests, 30 (31.6%) disappeared and were presumably removed by predators; three eggs (3.2%) did not hatch and 62 hatched successfully (65.2%). Johnson (1963) also reported an egg survival rate of 65% (N = 27 eggs). Of 62 nestlings, 24 (38.7%) were removed by predators or died in the nest, whereas 38 (61.3%) fledged. Overall nesting success from laying to fledging was 40.0% (38/95).

Using the exposure procedure (Mayfield 1961) to calculate success, the survival probabilities were as follows: survival of the egg to hatching = 0.638; hatching success = 0.954; survival of the hatchling to fledging = 0.619. The probability of survival from incubation through fledging was $0.638 \times 0.954 \times 0.619 = 0.376$ (37.6%). This value compares with a mean survival of 43% for nine open-nesting passerines (Nice 1943); 44.6% (King 1955), 65.6% (Walkinshaw 1966), and 36.4% (Holcomb 1972b) for Willow Flycatcher; and 65% for Western Flycatcher (*E. difficilis*) (Davis et al. 1963).

The number of young reared/nest was 1.6 ± 0.3 (38 fledglings/24 nests). Three pairs of flycatchers renested; hence, 21 pairs of adults reared an average of 1.9 young/pair. The mean number of Dusky Flycatchers fledged/successful nest was 2.7 ± 0.3 (38 young from 14 nests). Nest success was 58.3% (14 of 24 nests fledged > 1 young) with four nests (16.7%) producing four young, five (20.8%) producing three young, two (8.3%) producing two young, and three (12.5%) producing one young.

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